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RECOVERY OF SOIL MICROBIAL COMMUNITY STRUCTURE AFTER FIRE IN A SAGEBRUSH-GRASSLAND ECOSYSTEM

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ABSTRACT

Recovery of the soil microbial community after fire in a sagebrush-grassland ecosystem was examined using a chronosequence of four sites ranging in time since fire from 3–39 years. The successional stage communities examined included Recent Burn (3 years since fire, ysf), Establishment (7 ysf), Expansion (21 ysf), and Mature (39 ysf). Aboveground standing plant biomass increased with time since disturbance to the Mature stage where sagebrush became dominant over herbaceous species. Phospholipid fatty acid (PLFA) analysis was used to characterize the microbial community structure. Soil microbial community productivity generally appeared to be similar to the Mature site soil (39 ysf) within 7 years of fire. Diversity of PLFAs detected in soils, at both depths, increased from a low value of 29 at the Recent site to a high of 37 at the Establishment site and then decreased again to 31 at the Mature stage site. Canonical variates analysis indicated important disparities in microbial community structure at the four sites. Greatest disparities were observed in microbial community structure between the Recent and Establishment stages but greater similarity between the Recent stage and the sagebrush dominated Mature stage. This study emphasizes both short-term and long-term changes in the belowground community and suggests that soil microbial communities are highly resilient to disturbances after prescribed fire. Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS: canonical variates analysis; fire; microbial diversity; phospholipid fatty acid analysis; sagebrush-grassland; USA

INTRODUCTION

During the last few decades wildfires have increased in parts of the western United States (US) as have their impacts on western ecosystem and rangelands (Grissino-Meyer and Swetnam, 2000; Conard *et al.*, 2001; Hamman *et al.*, 2007). If the western states develop wetter winters and warmer summers throughout the 21st century due to global climate change, woody growth is expected to expand and increase fire risks (Rapp, 2004). As fire frequency and intensity increase, the importance of understanding the consequences of fires on plant and microbial communities and ecosystem function also increases. Severe fire can destroy above-and belowground communities and biomass, as well as alter abiotic environmental conditions. The action of both heat and ash modify soil chemical and physical properties (Diaz-Ravina *et al.*, 1992) and thus alterations in microbial populations may be expected following fire (Vazquez *et al.*, 1993). Intense fires cause significant loss of organic matter, deterioration of structure and porosity, considerable loss of nutrients through volatilization, leaching and erosion, and marked alterations of both biomass and specific composition of soil biotic communities (Certini, 2005). In addition, bulk density, pH, and water infiltration are usually impacted (Certini *et al.*, 2003).

Soil microorganisms are crucial to ecosystem function and significantly contribute to nutrient cycling, organic matter decomposition, plant nutrient uptake and maintenance of soil structure. Fire is known to alter soil microbial community composition and activity directly through heat-induced microbial mortality (DeBano *et al.*, 1998; Hart *et al.*, 2005) and ultimately modify soil communities by altering plant community composition through plant-induced changes in the soil environment (Hart *et al.*, 2005). Studies have shown that bacteria tend to be more resistant to heat induced by fire than fungi immediately following even moderate-intensity fires (Pietikainen and Fritze, 1995; Hart *et al.*, 2005), and microbial biomass is markedly reduced by fire, recovering in as long as 13 years in forest soils (Prieto-Fernandez *et al.* 1998). However, very little information exists regarding microbial community succession after fire over the long-term, and an

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understanding of both the short-and long-term impacts of fire on these organisms is important for elucidating the impacts of fire in an ecosystem (Hart *et al.*, 2005).

For decades, diversity and plant productivity relationships have played a pivotal role in ecosystem studies (Tilman, 1999; Chapin *et al.*, 2000; Mittelbach *et al.*, 2001; Hooper *et al.*, 2005). After disturbance, especially with the increase in plant productivity, microbial diversity increases rapidly as time progresses, peaking at some critical stage and then declining thereafter. Bai *et al.* (2007) observed that microbial species diversity increases at low levels of productivity and decreases at high levels of productivity.

Plant community structure is an important determinant of soil microbial community structure (Grayston *et al.*, 1998, 2001) and recovery of disturbed land depends on the development of plant communities over time. Furthermore, greater aboveground diversity harbored a larger microbial biomass than with homogeneous plant cover (Pinzari *et al.*, 1999; Fioretto *et al.*, 2009). Strong links between plant functional groups or species and soil microbial communities (Wardle, 2002) suggest that changes in vegetative community structure in the years following fire have the potential to be a more dominant factor influencing soil microbial community dynamics than the direct impact of the fire disturbance itself (Hart *et al.*, 2005).

Big Sagebrush (*Artemisia tridentata* Nutt.) is one of the most important plant species in the western United States (Wambolt *et al.*, 2001). Sagebrush ecosystems occupy over 62 000 000 ha in the region (Kuchler, 1970; West and Young, 2000) and fire events in upper elevation ecosystems initiate a predictable succession in these systems from perennial grass to sagebrush shrub (Cleary, 2007; Ewers and Pendall, 2008). Sagebrush shrubs form islands of fertility due to accumulation of organic matter in soil beneath their canopy, which results in greater soil nutrient concentrations, increased water holding capacity, water retention, microbial biomass and biotic activity as compared to areas between shrubs (Huber-Sannwald and Pyke, 2005). With occurrence of wildfire increasing in lower elevation sagebrush-grassland ecosystems in western North America (Thompson, 2007), information regarding fire impacts on ecosystem structure and function are crucial as are an understanding of how belowground ecosystem components recover from fire.

The objective of this study was to examine the soil microbial community response to and recovery from prescribed fire in a sagebrush-grassland ecosystem using a chronosequence of four burned sites. We hypothesized that (1) microbial community of a recently burned site would have lowest microbial biomass, diversity, and different community composition than the older sites, (2) saprophytic and arbuscular mycorrhizal fungi would have the lowest standing biomass and bacteria would have the greatest at the recently burned site, and (3) as primary productivity and standing plant biomass increase with time after fire so would fungal productivity and standing biomass.

METHODS

Study Site

This study was conducted in the Savory Creek watershed, a high elevation intermountain basin in south central Wyoming, 32 km east of the continental divide. Mean annual temperature in this area is 6·2–7·2°C and mean annual precipitation is 259–341 mm (Ewers and Pendall, 2008). All sites are located at similar elevation (2280–2310 m; Table I) and within 3 km of each other. Kuchler (1970) classifies vegetation in this area as Agropyron-Stipa-Artemisia shrubsteppe (Sagebrush-grassland ecosystem). Chronosequence sites were defined by the number of years since fire (ysf) at the time of sampling and were described by their stage of recovery after fire. The stages included a Recent Burn (3 ysf, burned in 2003), an Establishment stage (7 ysf, burned in 1999), an Expansion stage (21 ysf, burned in 1985), and a Mature stage (39 ysf, burned in 1967).

Table I. Ecosystem properties for a sagebrush fire chronosequence in Wyoming (Cleary, 2007). Standard errors are in parentheses.

	Recent	Establishment	Expansion	Mature
Age (ysf)	3	7	21	39
Elevation (m)	2309	2260	2283	2250
Location				
Latitude	41°18′ 13″N	41° 19’ 52″N	41° 21’ 48·9″N	41° 19’ 53″N
Longitude	107° 19′ 33″W	107° 24′ 2·4″W	107° 21′ 18″W	107° 24′ 3·9″W
Aboveground biomass ($g\,m^{-2}$)				
Herbaceous	120 (14)	160 (30)	190 (49)	39 (6·6)
Sagebrush	0·05 (0·03)	0·56 (0·29)	82 (30)	440 (37)
Number of plant species (count)	16	18	15	20
Soil characteristics (0–10 cm)				
SOC ($g\,m^{-2}$)	3300 (1200)	4400 (450)	4600 (14)	5100 (550)
Bulk density ($g\,cm^{-3}$)	0·79 (0·06)	0·9 (0·01)	0·78 (0·06)	0·82 (0·04)
pH	5·9 (0·1)	6·8 (0·1)	6·7 (0·1)	6·0 (0·1)

Sampling

Soil samples for microbial community analysis were collected in summer 2006 from 0–5 cm and 5–15 cm depths. The top 5 cm of soil was collected with a trowel and the 5-15 cm depth with a 2·5 cm diameter step probe. Three randomly oriented 45 m transects were set and soil samples were collected from four points in each transect at 0, 15, 30, and 45 m. Samples were placed in sealed plastic bags, stored on dry ice immediately after collection, and then returned to the laboratory where they were placed in a -20°C freezer until analyzed.

Soil PLFA Analysis

Phospholipid fatty acids (PLFAs) were extracted from 10 g soil samples using a modified Bligh-Dyer method (Bligh and Dyer, 1959; Frostegard and Baath, 1991; Blackwood and Buyer, 2004). Fatty acids were directly extracted from soil samples using a mixture of chloroform: methanol: phosphate buffer (1:2:0·8). PLFAs were separated from neutral and glycolipid fatty acids in solid phase extraction columns. After mild alkaline methanolysis, PLFA samples were qualitatively and quantitatively analyzed using an Agilent 6890 gas chromatograph (Agilent Technologies, Palo Alto, CA; Blackwood and Buyer, 2004) and Sherlock® software (MIDI Inc., Newark, NJ).

Individual PLFA signatures were used to quantify the abundances of specific microbial groups in soil samples. Gram positive bacteria were identified and quantified by the presence of Iso- and anteiso-branched fatty acids, Gram negative bacteria with monounsaturated fatty acids, and eubacteria with 15:0, 17:0 cyclo, 15:1 iso, and 17:1 iso and anteiso. Fungi were identified and quantified with 18:2 ω6c, actinomycetes with 10-methyl fatty acids and arbuscular mycorrhizal fungi (AMF) with 16:1 ω5c (Frostegard *et al.*, 1993; Cavigelli *et al.*, 1995; Zelles *et al.*, 1994, 1995). A study conducted by Olsson (1999) suggests that 30–60 per cent of 16:1 ω5c is due to gram-negative bacteria, the remainder, 40–70 per cent, may be presumed to be due to AMF. PLFAs were grouped into bacteria (Gram positive and Gram negative), fungi, AMF, and actinomycetes.

Microbial Diversity

Microbial community diversity was characterized in two ways, by the total number of different PLFA's and using the Shannon diversity index $H = -\Sigma^{n}_{i=1}\, p_i \ln (p_i)$, where n is the number of species and p_i is the measure of *ith* species proportional to total measure of all species (Zak *et al.*, 1994). In the case of our PLFA data, species are represented by identified fatty acids. Therefore, p_i is the concentration of *ith* individual fatty acid relative to the concentration of all fatty acids (Yao *et al.*, 2006).

DATA ANALYSIS

Statistical analysis was conducted using SAS 9·1 (SAS Institute, 2003). Two-way analysis of variance (ANOVA) followed by *post hoc* means separations using Tukey's Studentized Range (HSD) test was utilized to examine the significant differences among microbial community compositions. A multivariate method (canonical variates analysis) was used to compare soil microbial communities from the four different stages and to determine similarity among microbial communities in the different stage soils. In this analysis MANOVA identifies the linear combination of variables (referred to as canonical variates) best separating the soil microbial community structure at the different stages. The canonical variates are graphed to summarize group differences (Seber, 1984; Buyer *et al.*, 1999, 2002). All statistical analyses were accomplished at the $p < 0{\cdot}05$ significance level.

RESULTS

Vegetation and Soil Properties

Vegetation at the study sites shifted during succession after fire from dominance by perennial graminoids including *Pascopyrum smithii* (Rydb.) (Formerly *Agropyron smithii*) *A. Love* (western wheatgrass) and *Stipa* spp. (needleandthread grass) to dominance by *Artemisia tridentata* Nutt spp. *vaseyana* (Rydb.) Beetle (mountain big sagebrush; Ewers and Pendall, 2008). Herbaceous biomass was greater in the Recent Burn and Expansion stages (120–190 g m^{-2}) than at the Mature stage (39 g m^{-2}; Table I; Cleary, 2007). Big sagebrush shrubs were present only in small numbers and size at the Recent Burn and Establishment (0·05–0·56 g m^{-2}) stages, and were dominant at the Mature stage (440 g m^{-2}; Cleary, 2007).

All sites were located on <1 per cent slope, to minimize differences in soil texture and soil water content and movement. Soil texture in the top 15 cm was sandy clay loam, C content averaged 2–3 per cent, and pH was near neutral (Ewers and Pendall, 2008). Soil physical and chemical properties were similar across the chronosequence except for the top 0–10 cm of soil organic carbon (SOC) (Table I; Cleary, 2007). Bulk density was not significantly different over the chronosequence regardless of soil type. The Establishment and Expansion stages had the highest pH. Soil organic matter was higher in Expansion and Mature stages compared to the Recent and Establishment stages. In the top 0–10 cm SOC was lowest at the Recent Burn (3300 g C m^{-2}) and highest at the Mature stage (5100 g C m^{-2}).

Total Amount of PLFAs per Gram Soil

Soils from the four different successional stage sites had variable amounts of fatty acids. The Expansion and Mature

stages contained less total PLFA than the Establishment stage, but more than the Recent Burn stage. As evidenced in Figure 1, total PLFA content in the 0–5 and 5–15 cm depth at the Establishment stage was greater than all other sites. Soil from the Recent Burn stage contained significantly ($p < 0{\cdot}05$) less PLFA than other sites.

PLFA Biomarker Values and Ratios

Fungi

Like the general biomass pattern observed in Figure 1, mean values for amounts of both the fungal biomarker and the arbuscular mycorrhizal fungal biomarker were lowest in the soil from the Recent Burn stage (Figure 2a, b). Soil from the Establishment stage had a significantly greater ($p < 0{\cdot}05$) mean concentration (more than double) of both these biomarkers than soil from the Recent Burn. The Expansion and Mature stages had lower AMF biomarker compared to Establishment stage whereas for fungal biomarker, the Mature stage had similar fungal biomarker to the Establishment stage.

Actinomycetes

The same general pattern observed for total biomass PLFAs, was also exhibited by actinomycete biomarker PLFAs (Figure 2c). Soil from the Recent Burn stage contained the smallest amount of actinomycete biomarker, the Establishment stage had the greatest amount of actinomycete biomarker, and the oldest two stages concentrations intermediate between those of the Recent Burn and Establishment stages. It is interesting to note that, unlike the other PLFAs, mean concentration of actinomycete biomarkers was generally slightly greater at the 5–15 cm depth than the 0–5 cm depth.

Gram negative and Gram positive bacteria

Biomarker PLFAs for both Gram negative and Gram positive bacteria at both depths were at their lowest concentration in soil from the Recent Burn stage site (Figure 2d, e). Soil from the Establishment stage had significantly greater concentrations of both Gram negative ($p < 0{\cdot}05$) and Gram positive ($p < 0{\cdot}05$) bacterial biomarker PLFAs at both depths. Concentration of PLFA biomarkers for Gram negative bacteria in soil from the Expansion stage were significantly lower at both depths ($p < 0{\cdot}05$) than at the Establishment stage. Concentration of Gram positive biomarkers from the Expansion site were similar to the Establishment site at the 0–5 cm depth but were significantly lower than at the 5–15 cm depth. Gram negative bacterial biomarkers from the Expansion stage were found in significantly lower amounts than at the Establishment stage at both depths ($p < 0{\cdot}05$). Soil from the Mature stage had amounts of Gram positive biomarker PLFAs similar to the Expansion stage.

Ratio of PLFA fungal to bacterial biomarkers

The ratio of fungal to bacterial PLFA biomarkers were 0·43, 1·19, 0·86, and 1·26 at the 0–5 cm depth and 0·17, 0·45, 0·44, and 0·39 at the 5–15 cm depth in the Recent Burn, Establishment, Expansion and Mature stages, respectively. Values typically observed for the ratio of fungal to bacterial PLFA biomarkers in undisturbed sagebrush-grassland ecosystem surface soils (0–5 or 0–10 cm depth) are generally greater than 1 (Mummey *et al.*, 2002).

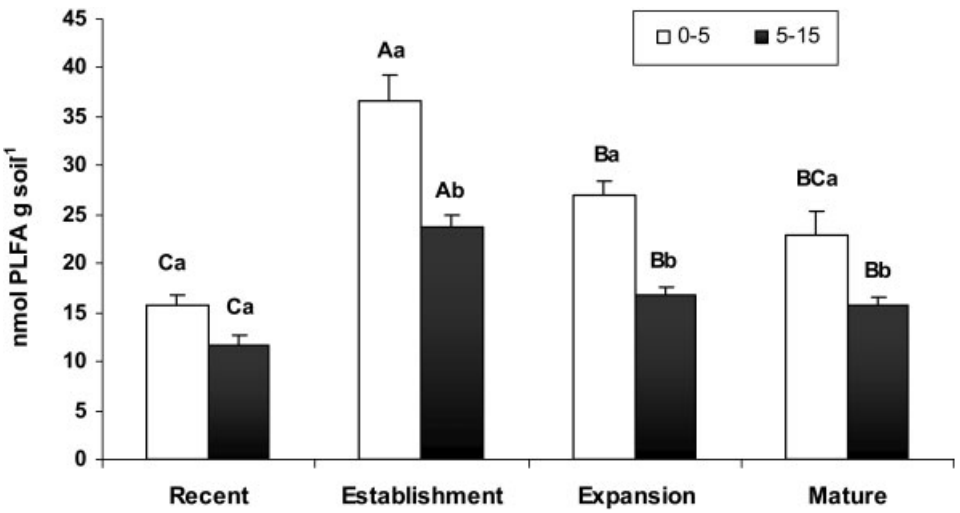

Figure 1. Total content of PLFAs at 0–5 and 5–15 cm depth. Different letters indicate significant differences ($p < 0{\cdot}05$). Error bars indicate standard error. Upper case letters indicate differences between stages and lower case letters indicate differences between depths at a stage.

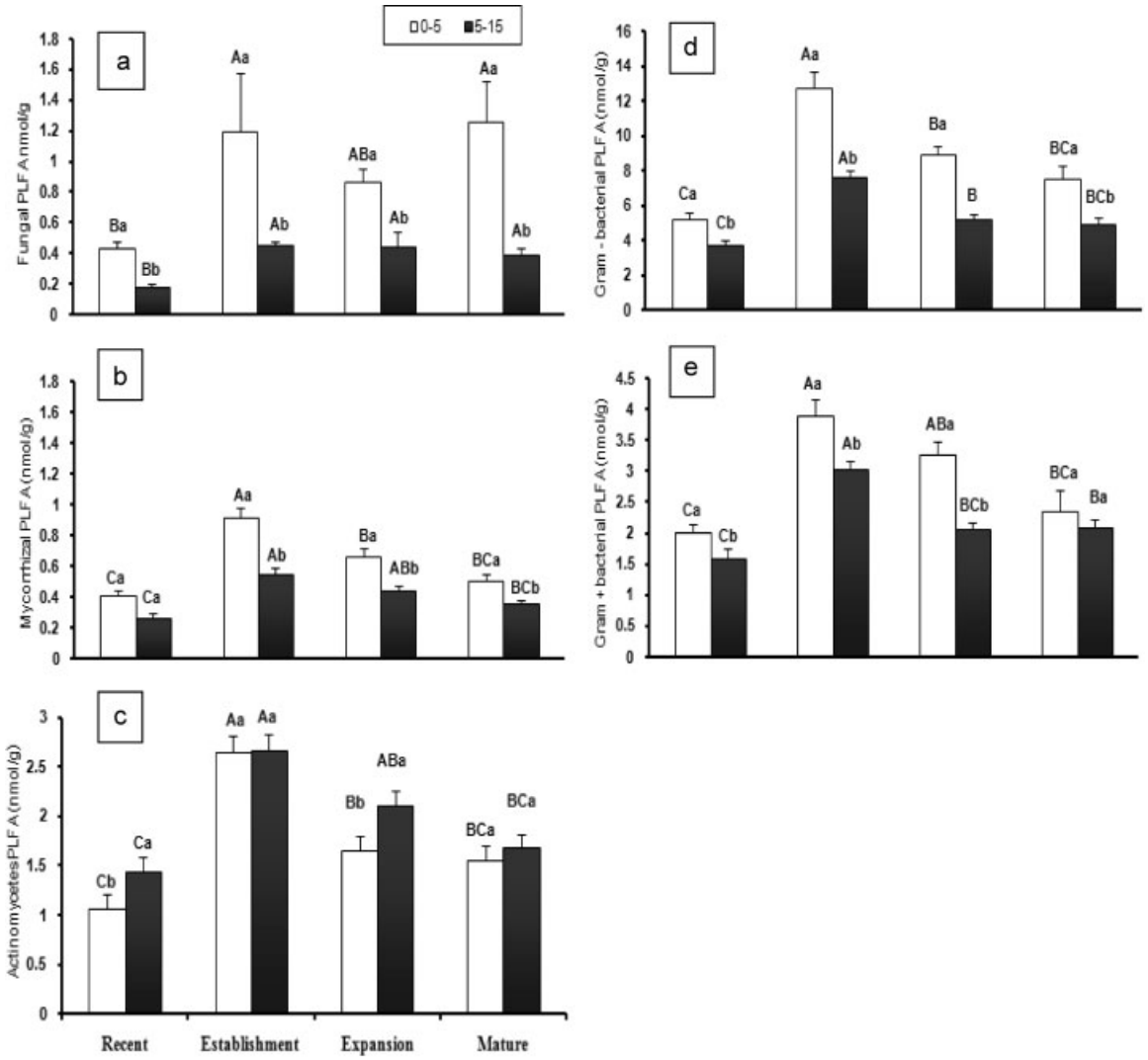

Figure 2. Fungal (a), Mycorrhizal (b), Actinomycetes (c), Gram − (d) and Gram + (e) bacterial PLFA at different depths from four sites. Upper case letters indicate differences between stages. Lower case letters indicate differences between depths at a stage. Different letters indicate significant differences ($p < 0{\cdot}05$). Standard bar indicates standard error.

Microbial Community Structure

Canonical multivariate analysis of variance indicates that soil microbial communities from all four sites share similarities (Figure 3) but, at least at the 0–5 cm depth, the community at the Recent Burn site may be the most distinct. This same analysis suggests greater similarities among communities at the 5–15 cm depth, especially between the Establishment and Expansion stages. The microbial community in soil at the Mature stage site was intermediate in terms of microbial biomass production compared to the Establishment stage site and the Expansion stage site.

The ability of the discriminant functions to distinguish between the younger and older burned sites on the basis of PLFA content was significant ($p < 0{\cdot}05$). For the 0–5 cm depth (Table II), canonical variate one discriminated the Establishment stage versus the Recent Burn and Mature stages, and canonical variate two discriminated the Recent Burn and Expansion stages versus the Mature stage. Soil from the Recent Burn stage was low in all PLFA biomarkers. The Establishment stage was influenced by relatively large amounts of Gram positive bacteria, Gram negative bacteria, actinomycete, and AMF biomarkers, but relatively low in fungal biomarker. Canonical variates analysis clearly demonstrated at both depths that concentration of fungal biomarker was lowest at younger sites and greatest at the oldest successional site.

For the 5–15 cm depth (Table III), results were similar to the 0–5 cm depth, but the differences were greater.

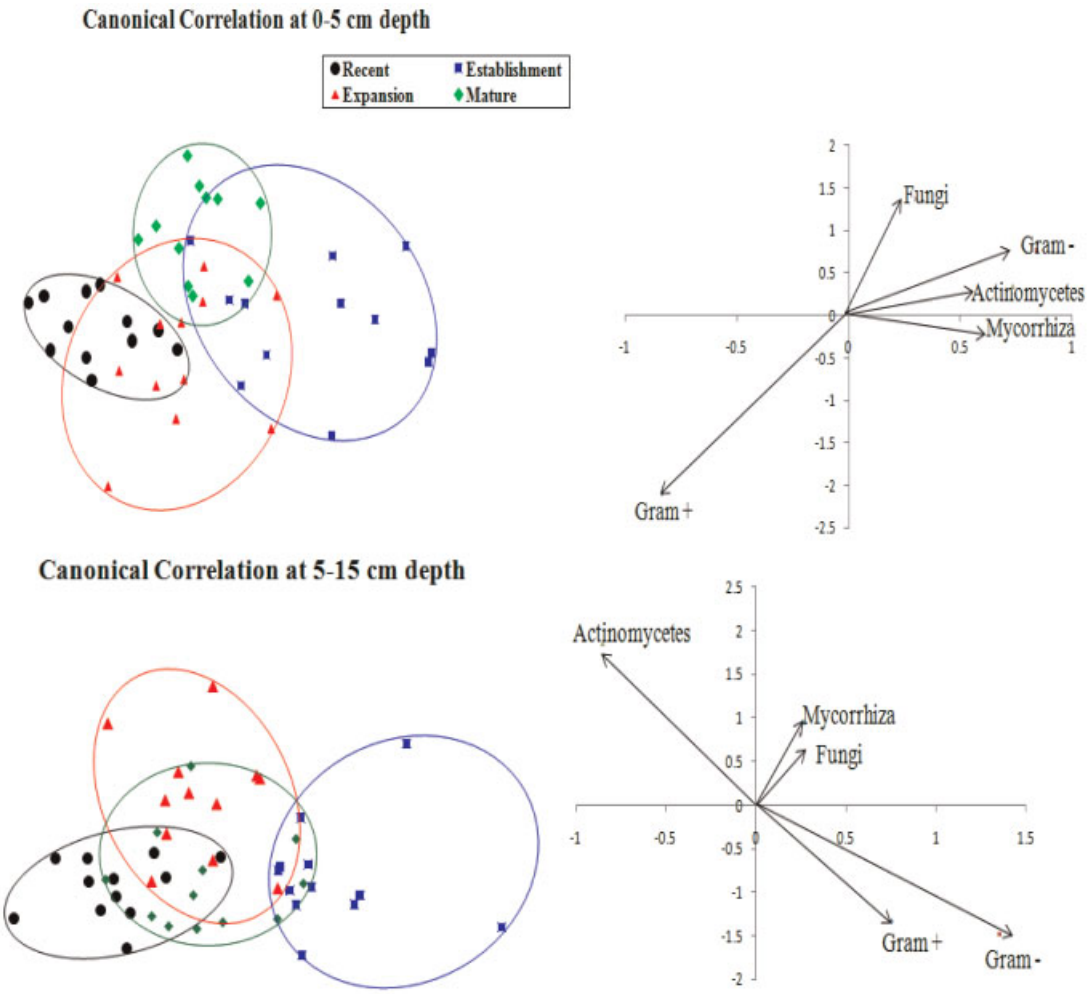

Figure 3. Canonical multivariate analysis of variance of PLFA biomarkers for Recent Burn, Establishment, Expansion and Mature sites at 0–5 cm and 5–15 cm depth. Vectors represent standardized canonical coefficients and indicate the relative contribution of each biomarker group to each canonical variate.

Table II. Structure matrix (Pooled with canonical structure) and function at group centroids for 0–5 cm depth

Canonical variate	One	Two
Structure loadings		
Gram positive bacteria	0·64	−0·07
Gram negative bacteria	0·89	0·13
Fungi	0·25	0·42
AM fungi	0·86	−0·004
Actinomycetes	0·85	0·20
Group centroids		
Recent	−1·31	−0·97
Establishment	2·05	0·15
Expansion	0·08	−0·98
Mature	−0·83	1·80

Table III. Structure matrix (pooled with canonical structure) and function at group centroid for 5–15 cm depth

Canonical variate	One	Two
Structure loadings		
Gram positive bacteria	0·86	−0·11
Gram negative bacteria	0·87	0·004
Fungi	0·36	0·39
AM fungi	0·69	0·31
Actinomycetes	0·62	0·22
Group centriods		
Recent	−1·76	−0·66
Establishment	2·04	−0·46
Expansion	−0·17	1·35
Mature	−0·10	−0·22

Canonical variate one discriminated the Establishment stage from the Recent Burn stage, and canonical variate two discriminated the Expansion stage from the Recent Burn and Establishment stages. The Recent Burn stage was low in all biomarkers. The Establishment stage was higher in Gram positive bacteria, Gram negative bacteria, actinomycetes, and AM, but relatively lower in fungi. The Expansion stage was very high in fungi and AM. The Mature stage was in between in respect to the microbes.

Canonical variate analysis of PLFA content of the different aged burnt sites was clearly able to discriminate between the younger and the older burnt sites on the basis of fungal, bacterial, actinomycetes and AM biomarkers (Figure 3, Tables II and III). It was shown from the discriminant analysis that at the 0–5 and 5–15 cm depths, fungal biomarker was lower in the youngest sites and highest in the oldest site.

Microbial Diversity

Both indices of diversity, number of different PLFAs and Shannon Diversity index (Table IV), show soil microbial community diversity varies significantly at the different successional stage sites examined. Diversity in soil from the 0-5 cm depth is relatively low at the Recent Burn and Mature stages compared to the Establishment and Expansion stages. At the 5-15 cm depth, soil from the Recent Burn site had lowest microbial diversity while soil from the Expansion and Mature sites was similar and intermediate between the Recent and Establishment stages.

DISCUSSION

Significant reductions after fire in microbial biomass have been reported for coniferous forests (Fritze *et al.*, 1993; Baath *et al.*, 1995; Pietikainen and Fritze, 1995; Villar *et al.*, 2004; Hart *et al.*, 2005; Hamman *et al.*, 2007) deciduous forests (Certini, 2005) and chaparral ecosystems (Dunn *et al.*, 1979, 1985). Recovery of soil microbial communities through time after fire is less well understood. Sampling soil along a fire chronosequence as we have done in this study captures short-term and long-term changes in the belowground community (Hamman *et al.*, 2007).

Table IV. Shannon index calculated from PLFA composition of soil microbial community ($p < 0{\cdot}05$). Upper case letters indicate differences between stages and lower case letters indicate differences between depths at a stage

Site	Diversity index	Total number of different PLFA's
0-5 cm depth		
Recent	2·64 Ba	29·0 CBa
Establishment	2·69 ABa	36·9 Aa
Expansion	2·73 Aa	34·6 ABa
Mature	2·60 Ba	31·5 Ba
5-15 cm depth		
Recent	2·37 Cb	22·2 Cb
Establishment	2·63 Ab	33·4 Ab
Expansion	2·49 Bb	26·6 Bb
Mature	2·49 Bb	25·7 Bb

Recovery of microbial biomass production at the burned sagebrush-grassland ecosystem sites is almost certainly related to plant community recovery, given the important interactions between plant and microbes, e.g., rhizosphere interactions, mycorrhizas, and the fact that a large proportion of organic litter (microbial substrate) in soil is of plant origin. In the big sagebrush steppe of the Western US, fire temporarily shifts vegetation from shrub-grass co-dominance to grass dominance (Wright and Bailey, 1982; Bates *et al.*, 2009). In our study, aboveground plant biomass data for the site (Table I) indicates productivity of herbaceous species (grasses and forbs) begins soon after fire and builds aboveground standing biomass to relatively high levels within 21 years. Only 3 years after burning, aboveground standing herbaceous biomass at the Recent Burn stage was already over 60 per cent of that at Expansion stage (Table I) indicating rapid recolonization by grasses and forbs which are known to produce more belowground biomass than aboveground biomass in semiarid environments (Brown *et al.*, 1998). Sagebrush is much slower to recover than herbaceous plants in terms of productivity and biomass (taking somewhere between 21 and 39 years).

Microbial productivity and standing biomass in soils appears to recover similar to Mature stage within 7 years of burning, indicating herbaceous plants provided new substrates and habitat. Unburned roots of sagebrush plants whose aboveground biomass was consumed by fire would also be provide substrate (as root detritus) in early years after fire. Microbial species richness was dependent on litter accumulation, but not on aboveground living plant, suggesting that there was no direct effect of productivity on diversity (Tilman, 1993).

Our results show the soil microbial biomass, as indicated by the total amount of PLFA in soil from low intensity fire, recovered like Mature stage sometime between 3 and 7 years after fire in a sagebrush-grassland ecosystem. The Expansion and Mature stages had similar microbial biomass content as relatively undisturbed sagebrush-grassland ecosystem soils we have examined previously (Mummey *et al.*, 2002; Rana *et al.*, 2007). In addition, our results are similar to the contention made by Pyne (1984), who reports that the effects of fire are temporary, with recovery in just a few years. Dumontet *et al.* (1996) examined fire effects in a forest ecosystem and reported that fire exerted a strong and lasting effect on microbial communities in soil where even

11 years after a fire, they found microbial biomass to be significantly lower than at unburned sites. In the forest ecosystem studied by Prieto-Fernandez *et al.* (1998), significant reductions in soil microbial biomass the first year after wildfire were followed by increases in following years. Villar *et al.* (2004) report negative impacts of fire on soil microbial biomass could persist for 4 to 13 years in forest ecosystems.

Biomarker PLFAs are specifically associated with microbial taxa at the family level or above and are not useful for assessing biodiversity at the species level but can provide a general indication of microbial diversity in soils (Kirk *et al.*, 2004). Soil PLFA content (Table IV) of burned sites examined in our study suggest microbial community diversity was lowest in soil from the Recent site, greatest in soil from the Establishment and Expansion successional stages after fire and intermediate in soil from the Mature stage site. The lowest mean value for number of different PLFAs in a soil (Recent Stage, 29) was almost 80 per cent of that from the soil with the greatest mean value of different PLFAs (Establishment Stage, 37) and 92 per cent of that in soil from the Mature Stage. This may indicate a minor reduction in microbial diversity as a result of fire, which then increases within 10 years to levels similar to soils in mature sagebrush stands. Plant community diversity showed no clear successional trends (Table I) with species richness values ranging from 15-20 and greatest species richness found at the Mature site.

The general trend of recovery through time after fire for all five microbial groups (Gram positive bacteria, Gram negative bacteria, actinomycetes, fungi, and AM fungi) was to have the lowest biomarker concentrations at the Recent Burn stage and highest in soil at Establishment stage. Biomarker concentrations for all groups in soil from both Expansion and Mature stages were similar to or lower than concentrations in soil from the Establishment stage. This indicates that microbial groups are increasing in productivity and are on a similar recovery track from 3–7 years after fire. At some point around 7 years after fire during or after the Expansion stage, soil microbial community biomass production declines. The disparity in behavior of microbial groups indicated by our data is that fungi in Establishment, Expansion, and Mature stages are not significantly different and do not follow the decreasing trend from Establishment to Mature stages. Also, actinomycetes appear to produce at least as much biomass in the 5–15 cm depth as in the surface soil (0–5 cm) which was also observed by Federle (1986), Fritze *et al.* (2000) and Fierer *et al.* (2003).

Canonical Variate analysis of PLFA data indicates there are important disparities in the relative proportions of the microbial groups in all the 4 stages. Biomass of all microbial groups is low at the Recent Burn stage. Bacteria (Gram positive and Gram negative) dominate the microbial community at the Establishment stage although there is also a relatively large amount of AMF biomass. As per Diaz-Ravina *et al.* (2006), soil heating decreased the PLFAs indicative of Gram positive bacteria and tended to increase the fatty acid associated with Gram negative bacteria. Increase in Gram negative bacteria in soils of a burned area was also seen by Mubyana-John *et al.* (2007). Microbial communities in soil from the two sites most temporally removed from fire were dominated by fungi. Our data support the hypothesis that bacteria appear to be generally more resistant to heat induced by fire than fungi (Pietikainen and Fritze, 1995). Our data show a peak in AM fungal biomass at the Establishment stage (7 ysf) which was contradictory to observations made by Klopatek *et al.* (1994) in their study indicating low AM abundance even 10 years after fire.

The soil organic carbon was lowest in Recent stage and greatest in soil from Mature stage. A study by Boerner *et al.* (2006) also reports the reduction of SOC after prescribed fire. The highest pH values were found in the Establishment and Expansion stages, which also had the highest microbial community structure. Hart *et al.* (2005) suggested that increases in soil pH following fire may increase the activity of at least some soil microorganisms.

CONCLUSIONS

Studies on the recovery of soil microbial communities through time after fire are scarce. This is of great concern to ecologists and land managers. We have attempted to capture both short-term and long-term changes in the belowground community by sampling soil along a fire chronosequence. Our results demonstrate that productivity of herbaceous (grasses and forbs) species begins soon after fire and microbial communities appear to recover between 3 and 7 years after fire, which indicates that herbaceous plants provided new substrates and habitat for soil microbial communities. Also, microbial groups examined increase temporarily in productivity, but the most interesting component is that there is a reduction over time back to Recent stage except for fungi and soils from 5–15 cm depth contained considerably less PLFA than 0–5 cm depth. Results from this study on microbial community recovery from prescribed fire suggest that soil microbial communities are highly resilient to disturbances.

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